



Niche-Relationships Within and Among Intertidal Reef Fish Species

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Niche-related processes (e.g., density or niche-breadth compensation and competition) are fundamental to a broad understanding of community ecology and ecosystem functioning. Most evidences of competition are from controlled indoor trials with few species, and it remains a challenge to estimate competition among multiple species in the field. Here, we analyze stable isotopes and distributional data from 51 fish taxa in six locations in the southwestern Atlantic to predict intraspecific trophic pressure (ITP) and the potential competitive strength among species in a trophic-based framework. We used two proxies built upon 2-dimensional isotopic space ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$), its predicted overlap, and fish density to calculate winner and loser taxa in potential paired interspecific competitive interactions. The intraspecific proxy indicated that cryptobenthic fishes are under high among-individual trophic pressure (high densities and small niche sizes). Also, cryptobenthic behavior together with feeding specialization and extremely small-sizes were the most important traits related to low success in interspecific simulations. Although cryptobenthic fishes face strong competitive pressures, there are some known inherent trade-offs to cryptobenthic life such as trophic and habitat use specializations. These seem to compensate and ensure coexistence among cryptobenthic fishes and non-cryptobenthic species. Habitat loss/degradation via urbanization, invasive species and climate-change-driven sea-level rise can reduce the suitability of habitat and increase competition on cryptobenthic species, especially in shallow reefs and intertidal shores.

Keywords: tidepool, stable isotopes, rockpool ecology, reef fish, competition

INTRODUCTION

Competition is one of the most important driving forces shaping life forms, from microbes to large-sized plants and animals (Gause, 1934; Simberloff, 1982; Connell, 1983; Xavier and Foster, 2007; Bonin et al., 2015). The understanding of how the struggle for space and resources occurs drew Darwin's attention on the mechanisms involved in the coexistence and contests within and among species (Darwin, 1859). In his seminal book Darwin dedicated one chapter to the discussion of the mechanisms behind one species becoming victorious over another and on the role of natural selection in a competition spectrum (Darwin, 1859). Since then, several studies on the issue

have argued over ways and means to assess competitive interactions (Lotka, 1925; Volterra, 1926; Gause, 1934; Hutchinson, 1961; MacArthur and Levins, 1967; Connell, 1983; Schoener, 1983; Simberloff, 1983; Huisman and Weissing, 1994; Tilman, 1994) but these processes remain laborious to measure, especially in a speciose framework.

Competition is directly influenced by life-history modes in plants, invertebrates and vertebrates. In many cases, complex life-history traits (e.g., pelagic larval duration, food acquisition modes, size of early recruits) may define the settlement and adaptation success of species facing potential competition (Schoener, 1968; Osenberg, 1989; Olden et al., 2006; Andrades et al., 2019a). Historically, the search for estimates of niche overlap (on a spatial or trophic basis) have shed light on competition measurements and supported the majority of ecological inferences regarding potential competition assessments (Hutchinson, 1961, 1978; MacArthur, 1968; Bonin et al., 2015).

More recently, stable isotopes-based Bayesian estimates have allowed the measurement of the Hutchinsonian niche components in an isotopic space (mainly $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) called the isotopic niche and ultimately represented by ellipses (Newsome et al., 2007; Jackson et al., 2011). Since then, isotopic models have been used to explore niche-relationships in terrestrial, freshwater and marine environments through the quantification of the overlap, or partitioning, of trophic niches among species. For instance, isotopic niche size and overlap among individuals of small mammals in the Queen Elizabeth national park (Uganda) lead to the conclusion that individual trophic specialization emerges from increased intragroup competition (Sheppard et al., 2018). Similarly, ichthyologists evaluate that on Caribbean reefs the invasive lionfishes (*Pterois* spp.) compete more directly with a native endangered grouper (O'Farrell et al., 2014). In intertidal ecosystems, stable isotope analysis has been useful to detect the intraspecific partitioning of the dietary niche in fish species and has clarified the niche expansion phenomenon driven by competition release in island communities (Andrades et al., 2019a,b). Thus, stable isotope models provide reliable assessments of niche-relationships, including potential competition, mainly for those cases hard to observe or measure in nature.

An historically good model to investigate resource sharing and competition in nature is species occupancy in intertidal shores (rocky and biogenic reefs). The zonation under different pressure gradients (e.g., exposure to air, predation and temperature) and limiting living space revealed strong competition strategies and complex coexistence modes for gastropods, echinoderms and algae (Connell, 1961; Paine, 1969, 1974; Underwood, 1984; Metaxas and Scheibling, 1993; Vaz-Pinto et al., 2014) and inspired Robert Paine to coin the “keystone species” concept that has enlightened the role of predators in the maintenance of species diversity balance (Paine, 1966). However, most studies focused on sessile or slow-moving species (Metaxas and Scheibling, 1993) and, in the case of fishes, were mostly based on indoor experiments using one or few species simultaneously (Szabo, 2002; Arakaki

and Tokeshi, 2011, 2012; Pajmans and Wong, 2017; Colella et al., 2019). Intertidal reef pools host fishes that exhibit diverse physiological, morphological and behavioral adaptations to the stressful life “between the tides” (Gibson and Yoshiyama, 1999; Martin and Bridges, 1999; Zander, 2011). Cryptobenthic fishes are a remarkably abundant fish-group that is typically composed of small-sized species strongly associated to the bottom and that present rich taxonomic and functional aspects (Brandl et al., 2018). In space-limited tidepools, high populational and specific density and elevated energetic demands would put these fishes into a particularly high intra- and interspecific competitive framework. Because pools are isolated from the sea during low tides they offer the possibility to acquire robust density data to be merged with resource and habitat use information. Thus, the appraisal of winner and loser species in potential competitive interactions and the relationships among species intrinsic individual-traits can allow the detection of vulnerable taxa (potentially inferior competitors) in a multi-species framework built upon scenario of increased competition intermediated by habitat loss/degradation through human impacts.

Here, we examine six fish assemblages in oceanic and coastal intertidal reefs to investigate which species traits are associated with competitive success under distinct scenarios. For this, we use stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures and fish density data to assess intraspecific trophic pressure (ITP) and simulate interspecific competition. Further, we determine what species are the competitors most prone to deleterious effect in pairwise simulated competition.

MATERIALS AND METHODS

Study Areas

Fifteen tidepools were sampled in each of six tropical intertidal reef sites ($N = 90$) within Brazilian waters. Three sites were located in oceanic islands: (i) Rocas Atoll ($03^{\circ}51' \text{ S}$; $33^{\circ}49' \text{ W}$), the only atoll in the South Atlantic (266 km off coast) built primarily by coralline algae, vermetid gastropods and hermatypic corals (Gherardi and Bosence, 2001); (ii) Fernando de Noronha Archipelago ($03^{\circ}50' \text{ S}$; $32^{\circ}25' \text{ W}$), 345 km from mainland, where rocky intertidal reefs are often associated with biogenic carbonate substrate composed by encrusting coralline algae; and (iii) Trindade Island ($20^{\circ}30' \text{ S}$; $29^{\circ}20' \text{ W}$), the most isolated insular environment within Brazilian territory (1,160 km off coast) sheltering biogenic and phonolitic rocky reefs. Trindade has the highest reef fish endemism rate (9.6%) among the Brazilian islands (Pinheiro et al., 2015). In these sites, tidepool water temperature and salinity often varies from 27°C to 35°C and from 35 to 41, respectively (Andrades et al., 2018b). The coastal intertidal reefs in our study were: (i) Salinópolis (Farol Beach; $00^{\circ}36' \text{ S}$; $47^{\circ}21' \text{ W}$) located in northern region of Brazil where coastline are dominated by mangrove forests and estuaries, despite the occurrence of rocky outcrops. Farol Beach comprises a sandy beach with sparse lateritic and biogenic intertidal reefs with tidepool water temperature and salinity varying from 31°C to 35°C and 36 to 41, respectively

(Andrades et al., 2018b); (ii) Jericoacoara (02°47' S; 40°30' W) located in northeastern Brazil where quartzite beachrocks makes of the intertidal reefs. Water temperature and salinity in tidepools varied from 24°C to 32°C and 35 to 41, respectively (Machado et al., 2015; Andrades et al., 2018b); and (iii) Anchieta (Castelhanos Beach; 20°49' S; 40°36' W) located in the southeastern region of Brazil with a flat intertidal reef composed mainly by encrusting coralline algae and stony coral skeletons with tidepool water temperature and salinity varying from 24°C to 35°C and 36 to 41, respectively (Macieira and Joyeux, 2011; Andrades et al., 2018b).

Fish Sampling and Laboratory Procedures

Fish were sampled in field expeditions performed during the dry seasons of 2014 (Rocas Atoll) and 2015 (the other sites). At each site, fifteen tidepools were chosen at random during the ebb tide providing there was no connectivity to the sea or to other pools. Specimens were caught using hand nets after application of the anesthetic clove oil (40 mg·l⁻¹ in ethanol), an efficient and selective method not inducing mortality in non-target fauna (Griffiths, 2000). Concomitantly to fish sampling, the topography and bathymetry of the tidepools were surveyed using a 10 cm × 10 cm grid for the measurement of the depth at each point of tidepool. Then, the tidepool volume (m³) was calculated by kriging. At each site, non-systematic (extensive) fish collections in tidepools other than those surveyed were carried out to increase the sample size for stable isotope analysis (see below) and to collect species not encountered during systematic sampling. After collection, individuals were frozen at -20°C in the laboratory, where abundance, total length and wet weight measurements were taken. For stable isotopes, muscle tissue samples were removed from the antero-lateral portion of the trunk, except for small-sized fish. Individuals with a total length under 30 mm (e.g., *Tomicodon* sp.), were used whole after removal of viscera, scales, fins, and head. All samples were dried in a standard laboratory oven at 60°C during 48 h, and then homogenized using a pestle and mortar.

Stable Isotope Analysis

Fish samples (ca. 0.5 mg ground tissues) from systematic and extensive collections were analyzed for stable isotope ratios of carbon and nitrogen using continuous-flow isotope ratio mass spectrometry in a Costech elemental analyzer coupled to a Micromass Isoprime isotope ratio mass spectrometer (EA/IRMS). The laboratory data were calibrated using NIST (National Institute of Standards and Technology) reference materials, PDB (Pee Dee Belemnite) for carbon and airborne N₂ for nitrogen. Stable isotope values are expressed using δ (delta) notation and parts per thousand (‰) as follows:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3,$$

where X is ¹³C or ¹⁵N and $R = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon and ¹⁵N/¹⁴N for nitrogen.

In order to avoid any bias resulting from chemical interference in the isotopic signatures, we did not extract lipids using chemical solvents, such as methanol-chloroform (Post et al., 2007; Boecklen et al., 2011). Given this, consumers δ¹³C signatures were corrected for lipid-rich samples (C:N > 3.5), following Post et al. (2007). Also, in order to avoid bias caused by ontogeny (Andrades et al., 2019a), whenever possible variation in body size was constrained among sites both within species and congeneric species (Andrades et al., 2019b).

Isotopic niche spaces (95% prediction ellipse area) occupied by species were estimated from stable isotope ratios (δ¹³C and δ¹⁵N) using the multivariate ellipse-based model “SIBER” (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011). Mean values of δ¹³C and δ¹⁵N, as well as niche areas are available in **Supplementary Table 1**. To verify potential niche overlap among species we calculated the overlap of the maximum likelihood fitted standard ellipses using the function *maxLikOverlap* based on 95% prediction ellipse area.

Fish Traits

We set seven traits for intertidal reef fishes based on information provided in literature for intertidal reef fish ecology (Gibson, 1982; Gibson and Yoshiyama, 1999; Griffiths, 2003; Andrades et al., 2018a,b), these were endemism, residency level, trophic group, level of competition within trophic group, habitat association on tidepool, cryptobenthic behavior, and body size. All species and trait categorization and information are in **Supplementary Table 2**.

Intraspecific Trophic Pressure

A proxy of the intensity of intraspecific trophic interaction pressure was determined by dividing the density of each fish species by its isotopic niche width, as follows:

$$ITP_i = \frac{FD_i}{SEAC_i},$$

where FD_i is the transformed (log+1) mean fish density (ind.m⁻³) of species i and $SEAC_i$ is the small sample size cored (i.e., core isotopic niche ellipses) of species i , containing the 95% prediction ellipse interval. This simple approach represents the density of a population in relation to the size of its isotopic niche size, with higher ITP values representing a greater degree of ITP in the species population. Higher ITP implies an abundant species with limited resource use, which a scenario of habitat loss and limited resource availability may pose a threat to the maintenance of population energetic needs. For these analyses we included all fish taxa that had their density estimated during the systematic tidepool surveys and had, at least, three individuals for isotopic niche width estimates.

Interspecific Competition (Species Competition Proxy)

We quantified species competition proxy (SCP) considering the amount of overlap in the isotopic niche between two species

in relation to the density of the focal species. Specifically, we calculated:

$$SCP_i = \left(\frac{SEAC_i}{(SEAC_i - Ov_{ij})} \right)^{-FD_i}$$

where Ov_{ij} is the overlap of the area of the corrected standard ellipse between species i and j that corresponds to the overlap of ellipse area. We were thus able to measure the effect of species i on species j and vice versa through:

$$\alpha_{ij} = \frac{SCP_i}{SCP_j},$$

where α_{ij} is the effect of species j on i . We only evaluated potential competition effects for pairs of species that presented some degree of overlap of their small sample size cored 95% prediction ellipses, otherwise, SCP_i would be equal to FD_i , which is meaningless. Based on the competitive interactions between species and the number of potential competitors, we identified the most successful competitors in each studied assemblage, that is, the species that had the greatest net potential effect in the pairwise comparisons, and, in turn, the species most vulnerable to potential competitive interactions (i.e., weak competitors). Only fish species collected in systematic samplings were included in the analysis since stable isotope signatures and niche area were estimated. Species that were only collected during the extensive surveys (i.e., not sampled in systematic surveys, and thus not considered in density estimates) were *a priori* considered losers when in potential competitive interaction with those (which overlapped niche areas) from systematic surveys.

Then, we computed the competitive success rate (%) of each species of the six studied sites and classified taxa as strong competitors (>66% success in paired simulated scenarios), regular competitors (33–66% success) and weak competitors (<33% success). Thus, we built a classification tree using log-linear models from the function *loglin* and “rpart” package (Therneau and Atkinson, 2018) to identify the best response variables associated to the predictor, where the competitive success rate was the dependent variable and the species traits defined *a priori* were the independent variables. The tree was pruned using the complexity parameter value to minimize the cross-validation error (Breiman et al., 1984; De'ath and Fabricius, 2000; Borcard et al., 2018). Also, a confusion matrix was extracted to inform on the classification accuracy and the Kappa Index of Agreement was used to evaluate the proportion of correct classification predicted at a rate higher than expected (Cohen, 1960). The statistical analyses were ran in R software (R Core Team, 2017).

RESULTS

Intraspecific Trophic Pressure

Altogether, 51 fish taxa from the six sites were evaluated for ITP. The magnitude of ITP is represented as the percentage of each taxon ITP proxy in relation to sympatric taxa in each site

(Figure 1). Overall, weak competitors (red-colored) were small-sized taxa belonging to typical cryptobenthic families (Blenniidae, Gobiidae, Labrisomidae, and Gobiessocidae).

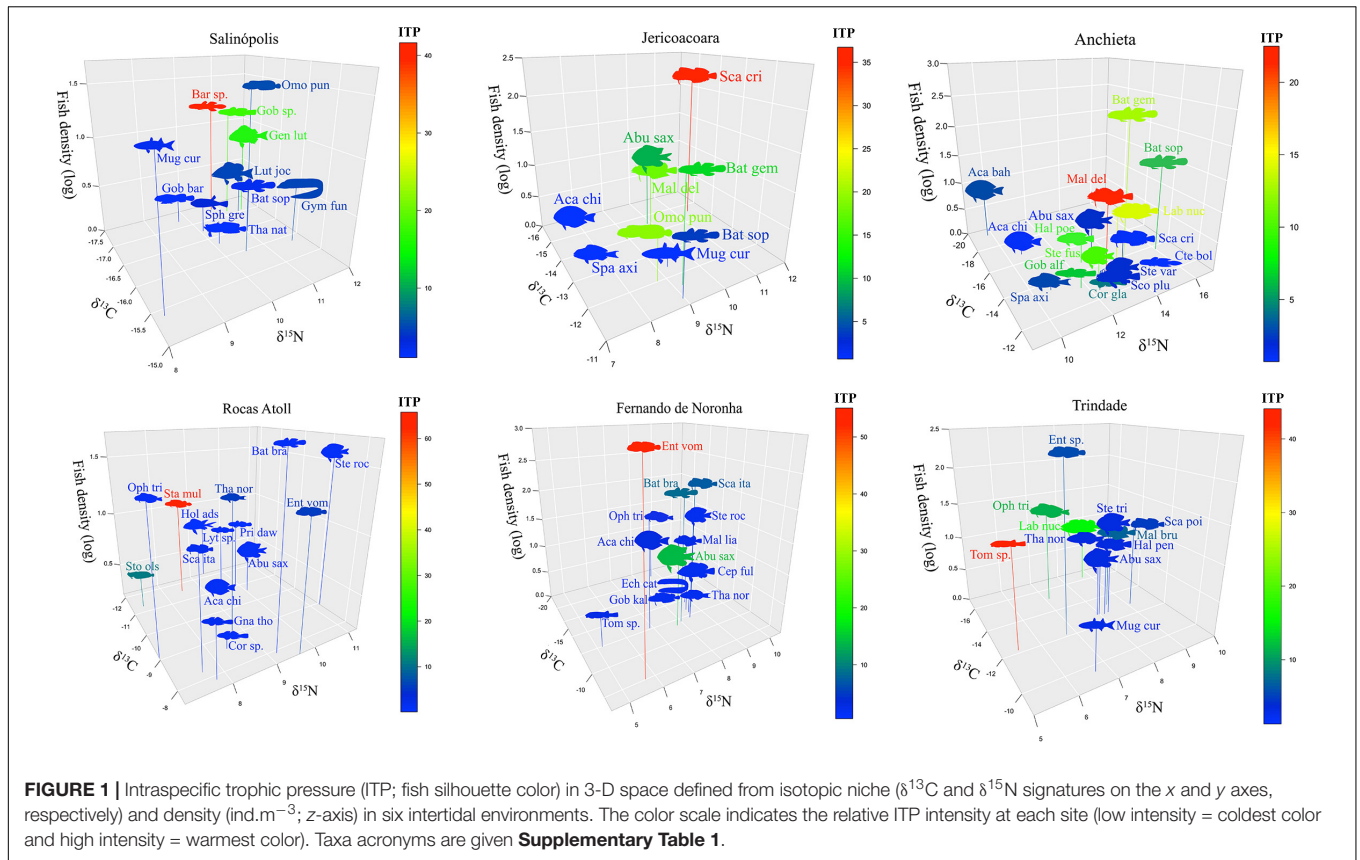
Interspecific Competition

The evaluation of interspecific interactions using the SCP indicated that the potentially inferior competitors were *Coryphopterus* sp., *Starksia multilepis*, and *Storrsia olsoni* at Rocas, *Abudefduf saxatilis*, *Gobioclinus kalisherae*, and *Entomacrodus vomerinus* at Noronha, *Malacoctenus brunoii*, *Tomicodon* sp. and *Mugil curvidens* at Trindade (Supplementary Figure 1), *Gobiesox barbatulus*, *Sphoeroides testudineus* and *Thalassophryne nattereri* at Salinópolis, *Omobranchus punctatus*, *Acanthurus chirurgus* and *Sparisoma axillare* at Jericoacoara, and *Sparisoma axillare*, *Stegastes variabilis*, and *Coryphopterus glaucofraenum* at Anchieta (Supplementary Figure 2).

Best-explanation tree model for SCP data included three traits: trophic group, body size and cryptobenthic behavior ($R^2 = 0.22$; root node error 0.60, Figure 2). The importance of these predictors in defining the tree structure was 38, 23, and 14%, respectively. Based on the confusion matrix (Supplementary Table 3), the percentage of the predicted response was 53.42 % (46.58 % of confusion) and the average kappa index was 0.27, an acceptable agreement. The primary split (1) separated the strongly competitive omnivore species from weakly competitive specialist species (carnivores, herbivores and micro-carnivores). The second node (3) splitted species in respect to their size and the subsequent split (6) in relation to their cryptic habit. Weak competitors (node 13) were cryptobenthic species of small (e.g., *Gobiosoma alfei* and *Tomicodon* sp.) and large (e.g., *Labrisomus nuchipinnis*) sizes.

DISCUSSION

We have shown that a diverse group of abundant species, the feeding-specialists of cryptobenthic behavior, is extremely vulnerable to interspecific competition and presents high rates of relative ITP for resources. Here, isotopic niche overlap between species was used to infer on potential interspecific competition. Although classical and contemporary approaches of niche overlap agree with this interpretation (Hutchinson, 1978; Eckrich et al., 2020), stable isotopes have limitations and how much niche overlap means to competition *per se* needs to be cautiously considered. Consumers with similar $\delta^{15}N$ signatures can feed upon different preys and similar $\delta^{13}C$ does not reflect obligatorily that both consumers are relying on the same resources. In fact, one of the main stable isotope analysis constraints is the lack of taxonomic refinement in potential prey identification (Newsome et al., 2007). On the other hand, competition can also exist between species whose realized niches do not overlap (Holt, 1987). Yet, in a space-limited habitat, such as intertidal reefs, potential competition among species cannot be underestimated, even among species belonging to different trophic guilds. For instance, typical territorial herbivorous reef fishes (e.g., *Stegastes* spp.) are able to compete for food with several other species acting as omnivorous (Zamprogno, 1989; Pimentel et al., 2018),

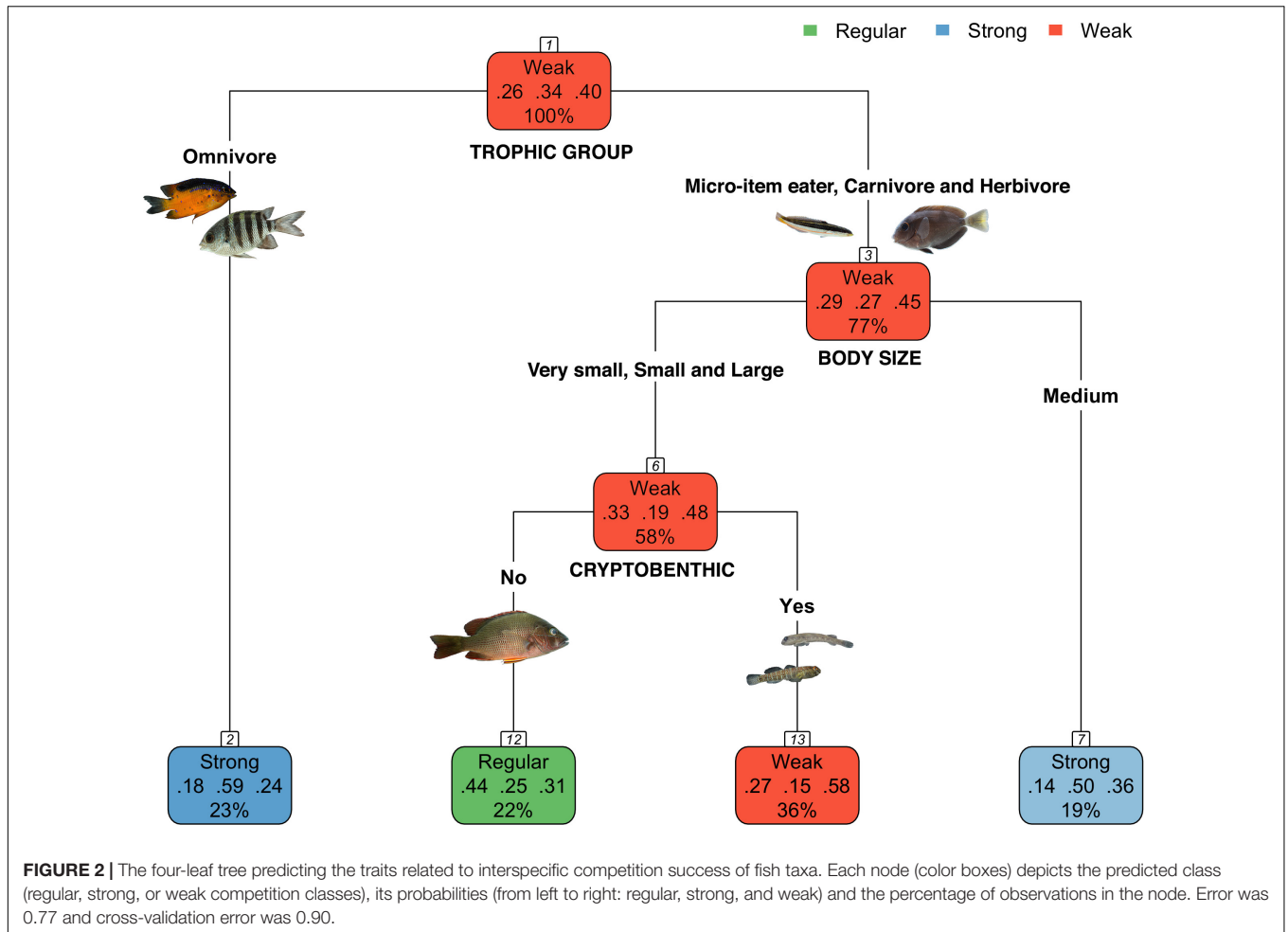


whereas resident gobies (e.g., *Bathygobius* spp.) expected to be carnivorous often consume also large amounts of algae (Zamprogno, 1989; Feitosa and Araújo, 2002). Despite its caveats, stable isotopes analysis overcomes the complexity of determining all competitive interactions and the accurate quantification of all axes of the niches hypervolumes. Our study is underpinned by evidences and case studies where isotopic niche overlap was considered a reliable and robust estimate of potential resource sharing or partitioning through the realized niches of species or individuals (Jackson et al., 2012; Fleming et al., 2015; Storero et al., 2020). Thus, isotopic niche overlap is closely linked to competition and furnishes plausible competition estimates (Colwell and Futuyma, 1971; Pianka, 2000; Sexton et al., 2017; Pastore et al., 2021).

The intrinsic biological resilience of the cryptobenthic species is associated with competition trade-offs and demographic dynamics. Very shallow reefs (<5 m depth) are stressful environments in which conditions widely fluctuate within the physicochemical (e.g., hydrodynamic and water salinity) and biological (e.g., primary and secondary production) spectra. It is expected that under high environmental variability rough competition scenarios may be relieved by competition trade-offs (Hutchinson, 1961; Duthie et al., 2014). In fact, such mechanisms can be observed from our intertidal assemblages. Rockpool blennies *Entomacrodus* spp. under high intra- and interspecific competitions in oceanic islands (mainly Noronha – **Figure 1**) persist as key-structuring species by occupying almost

exclusively isolated low-complexity tidepools of the high-shore (Andrades et al., 2018b). This displacement is so marked that very dense groups of *Entomacrodus* (**Figure 3A**) are common, even in small-sized pools. Possibly, *Entomacrodus* spp., a few small invertebrates and *Tomicodon* spp. converged toward this underutilized niche as it supports basal-resource exploitation while – essentially – persisting during the island existence (Macieira et al., 2015; Pinheiro et al., 2017; Andrades et al., 2019b). The stronger trophic pressure rates recorded for Noronha than Trindade endemic *Entomacrodus* can be explained by the abundant and speciose fish communities (Andrades et al., 2018b). These features are probably consequence of the larger intertidal area (ca. 60 km vs. 22 km total perimeter) and older origin of Noronha (~12.5 Ma vs. ~3.9 Ma; see Mohriak, 2020).

The only other sympatric fish that densely occupies the high-shore are *Tomicodon* spp. (**Figure 3B**; the species on the mainland, Trindade and Noronha/Rocas are distinct and only the first has been described, see Briggs, 1955; Macieira et al., 2015). These miniature taxa are often found in the surge zone, in small crevices or dead bivalve shells, under boulders or sea urchins (Karplus, 2014). Microhabitat specialization and competition release effects (Andrades et al., 2018b) allow higher abundance of *Entomacrodus* spp. and *Tomicodon* spp. in islands compared to mainland (Andrades et al., 2018a), agreeing to the MacArthur et al. (1972) “density compensation” hypothesis. Yet, as intraspecific competition increases in response to density compensation (Crowell, 1962; Pafilis et al., 2009), a



certain balance is probably maintained by species' capability to occupy micro-niches.

Other species under intense intra- and interspecific competition is the manyscaled blenny *S. multilepis* (Figure 3C), mainly in Rocas. This algae and anemone dweller inhabits rocky interstices. Its small mouth (Figure 3D) enables it to pick micro-items from algal turfs and fronds and its cryptic behavior favors avoidance of direct competition with stronger competitors. In fact, *Starksia* species presents high species richness at the regional-scale in the Caribbean (Baldwin et al., 2011), which is probably sustained by high levels of microhabitat partitioning among conspecifics through ecological speciation at small spatial scale (Rocha et al., 2005; Rocha and Bowen, 2008).

In relatively large-bodied intertidal reef specialists, ontogenetic niche shifts can drive microhabitat and dietary segregation to facilitate coexistence. The juvenile and adult of the cryptobenthic hairy blenny *L. nuchipinnis* (Figure 3E) act as two ecologically distinct species: they display distinct habitat occupancy, feeding modes and functional traits in order to maximize their food intake and reduce predation, including cannibalism by adults (Andrades et al., 2019a). Also, it is imperative to note that though the conventional definition of cryptobenthic species takes into account the

small-sized nature of the species (Brandl et al., 2018), morays like the chain moray *E. catenata* (Figure 3F) have a cryptobenthic nature while also being a top predator (see Andrades et al., 2019b). Such species perform highly vulnerable functions in reef environments due to their rarity and specific functional traits (nocturnal-feeding, sedentary) (Mouillot et al., 2013), but for few species daytime foraging also occurs (Sazima and Sazima, 2004). This justifies and brings attention to the presence of large vulnerable species in intertidal reefs (Figure 2).

Overall, cryptobenthic micro-specialists compensate their restricted niche, short-life span and high mortality with high reproductive rate and high larval input (Depczynski and Bellwood, 2006; Lefèvre et al., 2016). Brandl et al. (2019) estimate that this input is responsible to fueling reef environments with almost 60% of the fish biomass consumed, illustrating both this group vulnerability and its resilience to density-dependent processes such as intra- and interspecific competition.

Although cryptobenthic fish species can be found from the intertidal to mesophotic depths (<150 m) (Tornabene et al., 2016; Brandl et al., 2018), in our study many vulnerable taxa were restricted to the intertidal layer of only

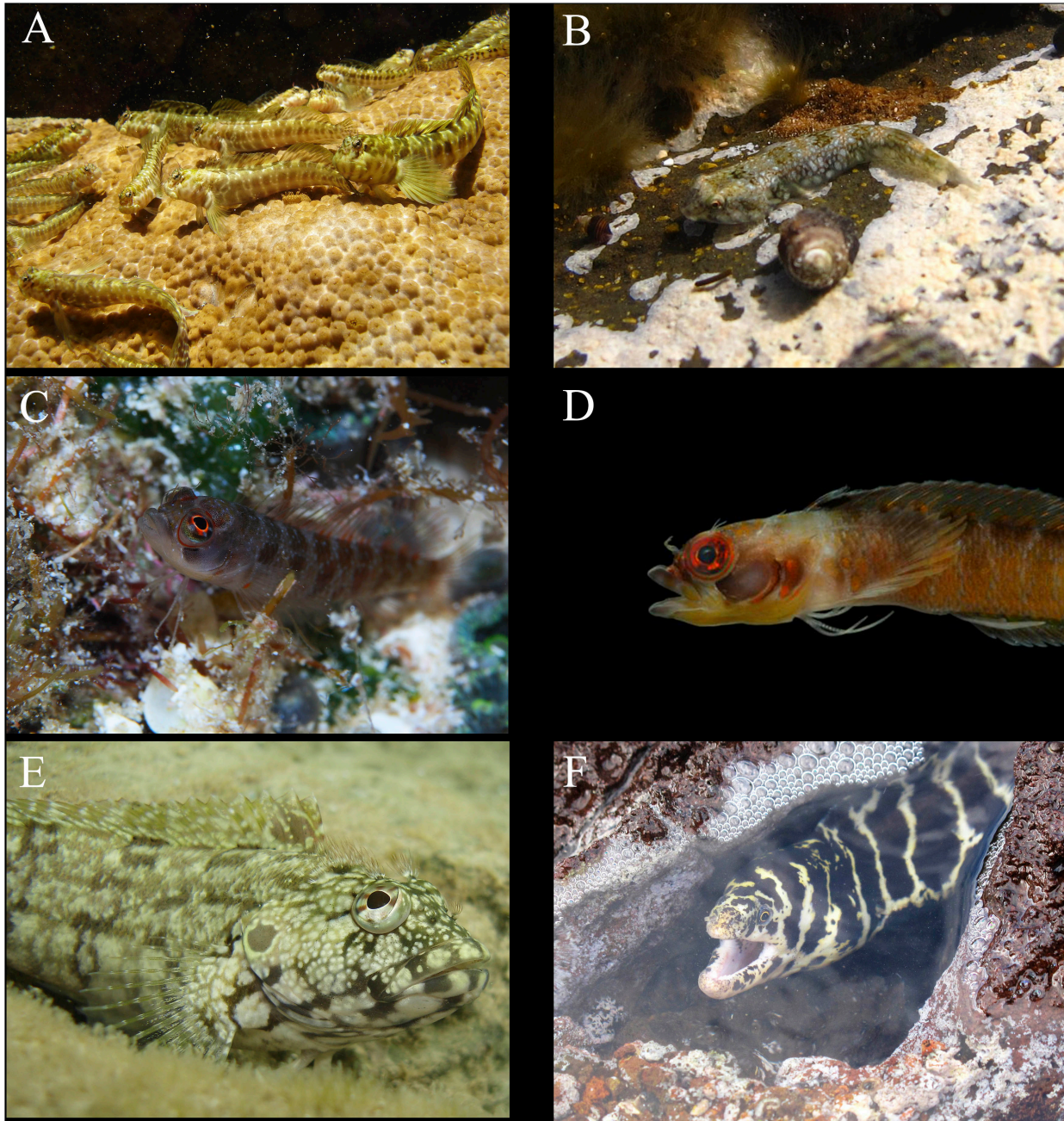


FIGURE 3 | Cryptobenthic intertidal reef fish of the South Atlantic Ocean. A dozen of *Entomacrodus vomerinus* lumped in a small tidepool (A). A solitary *Tomicodon* sp. in a rare moment out of a sea urchin crevice (B). *Starksia multilepis* within macroalgal interstices in an intertidal reef (C) and detail of the small mouth of 2 cm sized individual (D). Juvenile and adult of *Labrisomus nuchipinnis* (E) often inhabit intertidal reefs, but presented high niche partitioning of habitat and resource uses. The predator *Echidna catenata* (F).

a few centimeters to depths of less than 2 m. For instance *Tomicodon* sp. (Trindade), *S. multilepis* and *S. olsoni* (Rocas), *E. vomerinus* (Noronha) and *Barbulifer* sp. (Salinópolis) (see **Figure 1** and **Supplementary Figures 1, 2**) are under high selective competition pressures, despite their importance to the intertidal food chain (Andrades et al., 2019b). In a general competitive framework, an increase in the use of resources

by populations under high intraspecific pressure is expected (Giller, 1984; Svanbäck and Bolnick, 2007), a feature that would be especially relevant in species with limited capacity for niche adaptation. Therefore, intertidal cryptobenthic species having ecological traits (e.g., small body size or a particular habitat) that *a priori* limit trophic flexibility (e.g., exploitation of larger prey) or habitat change (e.g., toward greater depth)

would be under strong competition. It should be noted, however, that miniaturization facilitates singular spatial and trophic micro-niches occupancy among fishes (Miller, 1996; Brandl et al., 2018).

The idea that competitive interactions are responsible for biodiversity maintenance is well recognized. For the tropical marine fauna competition and its consequences may be the most important speciation processes in space-limited reefs (Schemske et al., 2009; Brown, 2014). Presumably, over the evolutionary time many tropical lineages have arisen, or at least presented high net diversification, to use low-quality diets instead of outcompeting strong competitors over high-quality resources (Harmelin-Vivien, 2002; Lobato et al., 2014). However, strong competition does not allow inferring detrimental effects over (expected) inferior competitors. Actually, niche overlap *per se* does not necessarily translate into interference effects but only in shared requirements over resources. No evidence for interference process limiting some species was detected in the present study but a general rule was clearly manifested: more-efficient specialists probably emerge to compensate the overpressure of generalists. In fact, while fine-grained experiment studies can demonstrate the immediate effects of competitive interactions they often are limited to a few species and local patterns. The model chosen for the regression tree presented a satisfactory result to estimate the competitive success of fish. However, other elements than those we used to build the model may have high relevancy and could have contributed to increase the observed fit. Some functional traits not included, because not sampled or considered secondary, may not be irrelevant to interactions. Further studies are needed to ascertain whether the insertion of other life-history traits (e.g., size classes and resource availability for each taxa or fish-group) can improve the fit of theoretical models. Finally, we used data from six locations, so regional differences in environmental characteristics may drive the importance of interactions between species in the communities. Further studies must consider, in addition to isotopic niche overlap, quantify prey-specific contribution through mixing models to best infer on potential overlap or partitioning of resources among consumers.

The costs of living under high competition pressure involve many deleterious effects such as low reproductive fitness and high energetic allocation in food searching, contest behavior and predation avoidance (Brieffa and Sneddon, 2010; Bonin et al., 2015; Forrester, 2015). Here, using stable isotopes allied to density data of more than 50 reef fish taxa, we demonstrated that high intra- and interspecific competition levels are centered over small-sized specialists, mostly belonging to cryptobenthic families. We also discussed a number of mechanisms that facilitate the coexistence of cryptobenthic fishes in an extremely fluctuating and competitive environment such as intertidal reefs. Nevertheless, anthropogenic impacts (e.g., biological invasion, urbanization, sea-level rise) can propel these taxa into risky scenarios of competition increase. Further studies must focus on fine-scale niche partitioning among taxa in order to enlighten the trophic plasticity and selective process upon target resources.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: The dataset will be published as part of a data paper soon. Requests to access these datasets should be directed to RA, ryanandrades@gmail.com.

ETHICS STATEMENT

The animal study was reviewed and approved by the UFES' Ethics Committee (CEUA-UFES; Protocol 29/2016). All specimen collection was licensed by Instituto Chico Mendes de Conservação da Biodiversidade/MMA – Brazilian Ministry of the Environment, through the SISBIO system.

AUTHOR CONTRIBUTIONS

RA, J-CJ, RM, and TG designed the study. RA, J-CJ, JR-F, RM, and TG collected the data. RA, BG, AJ, and TG developed the analysis. RA analyzed the data and wrote the manuscript. All authors revised and contributed to the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.659579/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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